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SEASONAL VARIATION IN THE ONSET OF EGG LAYING IN A PRIMITIVELY EUSOCIAL WASP: IMPLICATIONS FOR THE EVOLUTION OF SOCIALITY

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When freshly eclosed females of the primitively eusocial wasp, *Ropalidia marginata* are isolated into individual cages, only about half of them build nests and lay eggs and those that do so take a long and variable amount of time (Mean $\pm$ S D $= 66 \pm 37$ days) before they lay their first egg. Part of the reason for this delay is because, when kept in isolation, no wasp begins to lay eggs during a period of approximately 82 days from mid - October to early January. Wasps maintained at a constant temperature of $26 \pm 1°C$ however initiate egg laying throughout the year, suggesting that the low temperatures during mid - October to early January may be at least one factor that makes this period unfavourable for wasps maintained at room temperature. Egg laying continues more or less normally throughout October—January however, in all natural and laboratory colonies studied. Natural colonies of *R. marginata* are initiated throughout the year and often by groups of females. Huddling together is a striking feature of the wasps especially on cold mornings. We therefore suggest that the isolated animals in our experiment are unable to lay eggs during the coldest part of the year because of their inability to huddle together, share metabolic heat and perform "co-operative thermoregulation". Such "co-operative thermoregulation" may thus be another factor that facilitates the evolution of sociality.

(*Key words:* social wasp, *Ropalidia marginata*, seasonal variation in egg-laying, evolution of sociality, thermoregulation)

INTRODUCTION

In many primitively eusocial wasps and bees that lack morphological caste differentiation, a group of females nest together, of which one individual assumes the role of the queen while the others become workers and usually die without reproducing (WILSON, 1971; MICHENER, 1974; ROSS & MATTHEWS, 1991). A question of obvious interest is whether differentiation into queens and workers takes place entirely in the adult stage or whether there are any pre-imaginal effects that influence such differentiation. In an attempt to answer this question using the primitively eusocial wasp *Ropalidia marginata* (Lep.) (Hymenoptera : Vespidae), a large number of wasps were isolated into individual cages at eclosion, and thus rescued from any possible suppression of egg laying by conspecifics. A clear pre-imaginal caste bias was found because only about half of the 299 animals so tested built nests and laid eggs while the others died without doing so (GADAGKAR *et al.*, 1988, 1990). An intriguing observation in these experiments is that the time taken by the egg-layers to initiate nests and start laying eggs is often very long and variable.

Here we present results which suggest that part of the reason for the delay in the initiation of egg laying is that low temperatures in the months of November and December are not conducive to the initiation of egg laying by isolated females.

MATERIALS AND METHODS

For all experiments described in this paper, as for those described in the two earlier papers (GADAGKAR *et al.*, 1988, 1990), we have used freshly eclosed females of the primitively eusocial wasp, *R. marginata* whose biology and social organization are described elsewhere (GADAGKAR, 1991 ; GADAGKAR *et al.*, 1982; GADAGKAR & JOSHI, 1983). Naturally occurring nests were collected from around Bangalore (13° 00' N and 77° 32' E), cleared of adults and maintained in the laboratory. Females eclosing from these nests were tested for their ability to lay eggs by isolating them into individual 22 × 11 × 11 cm ventilated plastic jars. Each animal was provided with a piece of soft wood as a source of building material and an *ad libitum* diet of final instar *Corcyra cephalonica* (Staint.) (Lepidoptera : Pyralidae) larvae, honey and tap-water from the same source. All animals were observed for signs of nest building and egg laying every day. One set of animals was maintained in a well ventilated room and allowed to experience natural variations in temperature and light-dark cycle. The daily minimum and maximum temperature were however recorded. The other set of animals was maintained at a constant temperature of 26±1°C in an incubator. Since our main interest was to detect the ability or the lack of it, of the animals to develop their ovaries and lay eggs, the wasps were killed on the day they laid their first eggs. Our experimental procedures are described in more detail by GADAGKAR *et al.* (1988).

RESULTS

Time taken to initiate egg laying

A total of 299 female wasps were tested for their ability to initiate nests and lay eggs in experiments conducted at room temperature (GADAGKAR *et al.*, 1988, 1990). Of these, 150 wasps built nests and laid eggs. The time taken by these wasps to start laying eggs ranged from 14 to 218 days after eclosion. The distribution of these "waiting times" which has a mean of 66 days, a standard deviation of 37 days, and a median of 62 days is shown in Fig. 1.

Seasonal variation in the onset of egg laying

Why do some wasps take so long to start laying eggs? In an attempt to answer this question, we have examined the variation in the number of wasps that start laying eggs in each month. This brings out the rather unexpected result that no animal started laying eggs in the months of November and December although large numbers of wasps were alive during these months (Fig. 2). Over the 5 winters that these experiments were conducted, no egg layings were seen between 18th October and 9th January. It therefore appears that at least part of the reason for the delayed initiation of egg laying is that there is a fairly long unfavourable period of about 82 days during which the wasps do not start laying eggs.

Surely there would be some inherent delay in the onset of egg laying caused by the time required to attain reproductive maturity, but the long unfavourable period during winter could add to the delay observed. For instance, some animals may otherwise be ready to lay eggs during November and December but may have to wait till the unfavourable period passes before they can start laying eggs. This conjecture is supported by the distribution of "waiting times" shown separately for animals that lay eggs in the same year as their eclosion (without getting caught in winter) and those that wait for winter to pass before laying eggs (Fig. 3). The

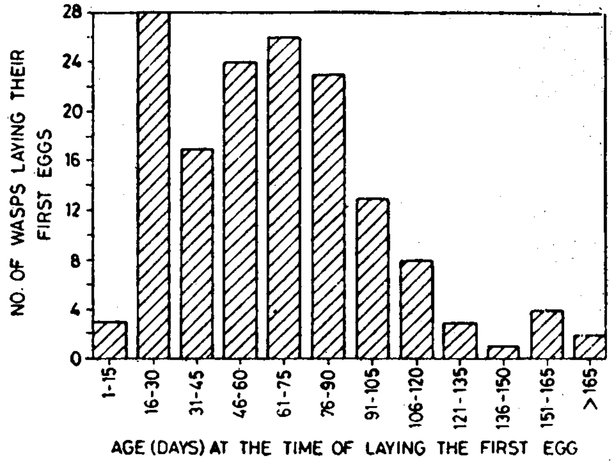

Fig. 1. Frequency distribution of wasps in different age classes at the time of laying their first eggs. (Mean = 66, S. D. = 37 and Median = 62).

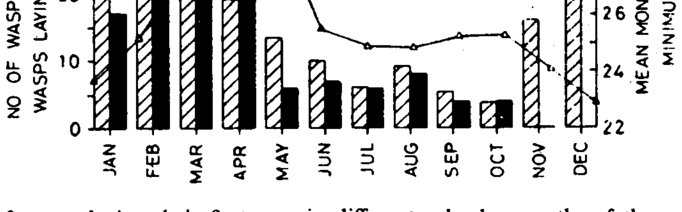

Fig. 2. Number of wasps laying their first eggs in different calendar months of the year (shaded bars). Variation from month to month in this regard should be interpreted in relation to the number of wasps alive during that month from among which animals could start laying eggs. This is shown as the number of wasp days for each month which is computed as the sum of the number of wasps alive during each day in that month (hatched bars). Data are pooled for all 5 years. Notice that no wasp initiated egg laying in the months of November and December although large numbers of them were alive during these months. The mean monthly maximum and minimum temperatures recorded during the experiment and averaged over years for each month are also shown.

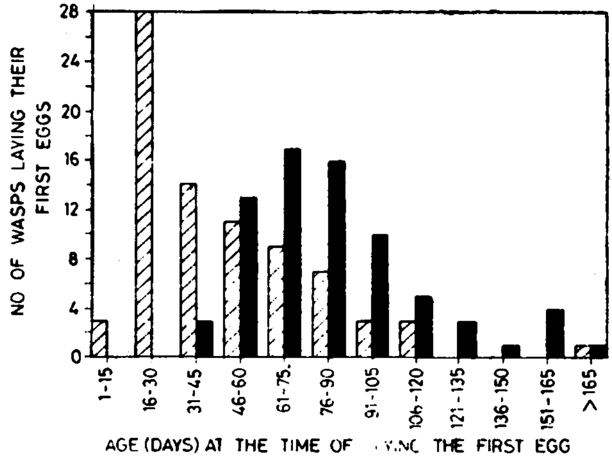

Fig. 3. Frequency distribution of wasps in different age classes at the time of laying their first eggs are shown separately for animals that initiate egg laying in the same year as their eclosion (without getting caught in winter) (hatched bars) (mean=48, S. D. = 31 and Median=40) and for those that wait for winter to pass before laying eggs (shaded bars) (Mean=85, S. D.=33 and Median=79). The two means are significantly different from each other (Mann–Whitney U test, $p<0.0001$).

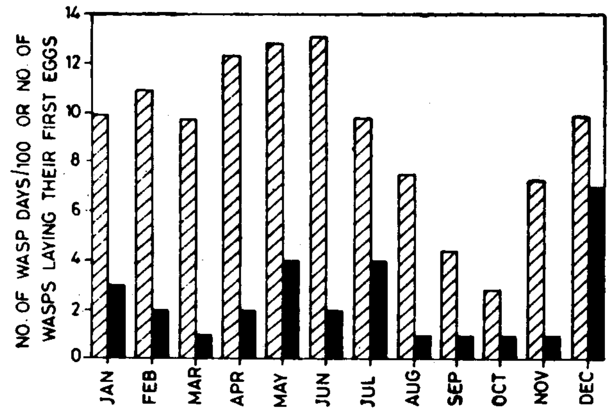

Fig. 4. Number of wasps laying their first eggs in different calendar months of the year (shaded bars) and number of wasp days for each month (defined in legend to Figure 2) (hatched bars) in the experiment conducted at a constant temperature of 26±1°C. Notice that here some animals initiate egg laying in November and December unlike in the experiment at room temperature (Fig. 2).

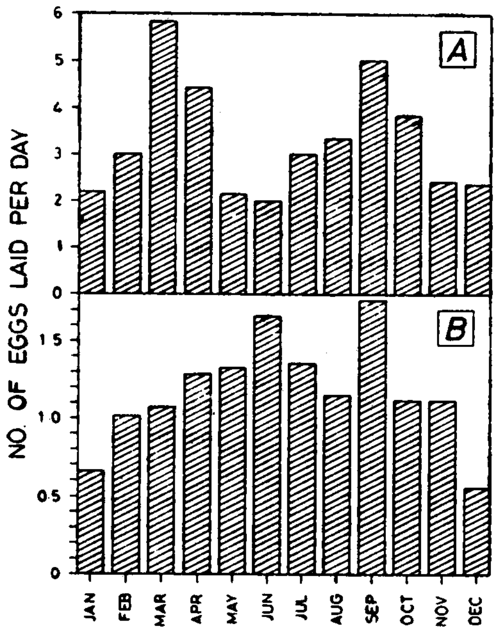

Fig. 5. A: Number of eggs laid per day during different calendar months averaged over four natural colonies which were observed approximately once in two days for about two years. These colonies had 20 or more females during most of the period under observation and a single egg-layer at any given time, B: Number of eggs laid per day during different calendar months averaged over four laboratory colonies which were observed daily for about a year. These colonies had 10 or more females during most of the period under observation and a single egg-layer at any given time.

former distribution (Fig. 3, hatched bars), which has a mean of 48 days represents the inherent delay that may be because of the time taken to attain reproductive maturity. The latter distribution (Fig. 3, shaded bars), which has a mean of 85 days represents the artificially inflated delay due to the unfavourable winter. The resultant mean "waiting time" of 66 days for the total population (Fig. 1) is significantly greater than the inherent mean "waiting time" of 48 days (Fig. 3, hatched bars) (Mann-Whitney U test, $p < 0.0001$). Why should November-December be unfavourable? A particularly striking correlate of seasons is of course temperature. Indeed, mid-October to mid-Janaury is the coldest part of the year in Bangalore as seen from the maximum and minimum temperatures recorded during the experiment (Fig. 2).

Wasps reared at constant temperature

Although many other factors vary with the seasons, a plausible hypothesis is that the period between mid-October and early January is unfavourable because of the low temperature prevailing at this time. To test this hypothesis, we have repeated the experiment at a constant temperature of 26 $\pm$1°C throughout the year in an incubator. The results of this experiment show clearly that the low temperature during November-December must be a major factor in making this period unfavourable. Several animals initiaited egg laying in the month of December when the wasps were reared at constant temperature (Fig. 4).

Comparison with Natural and Laboratory colonies

The fact that no animal ever started laying eggs in the months of November-December out of the 150 egg-layers in the experiments at room temperature is rather surprising. There is no apparent cessation of egg laying activity in several natural and laboratory colonies that we have observed from time to time (Fig. 5).

DISCUSSION

When female wasps of the primitively eusocial species *R. marginata* are isolated into individual cages at eclosion, only about half of them initiate nests and lay eggs. Among those that do so, there is considerable delay in the time taken to build nests and start laying eggs. At least part of this delay is because a period of about 82 days during late October to early January appears to be unfavourable for the onset of egg laying. But isolated animals initiate nests and lay eggs during November-December when they are kept in an incubator at constant temperature. Although there may be other differences between the conditions experienced by animals kept at room temperature and those in the incubator, temperature is an obvious one. We therefore suspect that the low temperature during mid-October to early January is at least partly responsible for the unfavourableness of this period. Egg laying continues at an appreciable rate however, during November-December in all natural colonies that we have observed. It is true that the animals in our experiment could not raise their body temperature by flying out and basking in the sun as animals in natural colonies can, but we rule out this as a critical factor because egg laying continues more or less normally during November-December in laboratory colonies too. A major difference between the animals in our experiment on the one hand and those in laboratory and natural colonies on the other, is that the former are isolated while the latter are in groups. It is therefore a reasonable hypothesis that the animals in our experiment did not lay eggs during the coldest part of the year because of their inability to huddle together with conspecifics, share metabolic heat and perform what might be called "co-operative thermoregulation".

The final test of this hypothesis must of course come from measurements of body temperature of isolated animals and those in groups at different temperatures. Although such measurements are presently beyond the scope of our laboratory, we have several reasons to believe that the strategy of "co-operative thermoregulation" is available to female *R. marginata* to raise their body temperatures, develop their ovaries and lay eggs during an otherwise unfavourable period. (1) Approximately 70% of the colonies are initiated by groups of foundresses whose number may be as high as 20, thus making "co-operative thermoregulation" possible (GADAGKAR *et al.*, 1982). (2) Nests are initiated throughout the year including the winter months suggesting that initiation of egg laying is possible during the winter months (GADAGKAR *et al.*, 1982; unpublished observations). (3) Both the phenomena of huddling together and the effect of temperature on the behaviour of the wasps are clearly evident during our attempts to collect colonies of *R. marginata* for experimental work. We find that almost all the wasps are huddled together, often behind the nest, in the early hours of the morning (before 6.00 a. m.) when we collect the colonies. The huddling is much more striking during winter or on otherwise colder mornings, when collecting a colony is relatively easy. During summer months or on otherwise warmer mornings, the wasps are easily disturbed, come to the front of the nest and even fly out and sting us, thus making collection difficult (GADAGKAR *et al.*, unpublished obsevations).

At the heart of most theories attempting to explain the evolution of insect sociality is an asymmetry in the productivities of solitary nesters and joint nesters. Defence against predators and parasites (LIN & MICHENER, 1972; GIBO, 1978; STRASSMANN *et al.*, 1988) and a greater ability to resist nest usurpation by conspecifics (GAMBOA, 1978) and better fitness returns in the face of high adult mortality and long brood-developmental times (QUELLER, 1989; GADAGKAR, 1990 b) are commonly cited reasons for the better performance of multiple-foundress associations as opposed to solitary individuals of wasps and bees. On the basis of the results reported here, we wish to suggest "co-operative thermoregulation" as yet another factor that would favour group nesting. We also wish to point out that both the above hypotheses we have considered namely, the possibility of wasps raising their body temperature by basking in the sun and of their doing so by "co-operative thermoregulation" have parallels in behavioural mechanisms for thermoregulation known for other insects (CASEY, 1981). Finally, we emphasize that if an advantage of group-living based on "co-operative thermoregulation" can be discerned in Bangalore where the winter minimum temperature rarely goes below 15°-20°C, such an advantage should be substantial at other latitudes where the winters are much colder.

There is yet another difference between the animals in our experiment and those in natural and laboratory colonies. Our data pertaining to natural and laboratory colonies reflect the ability of wasps having already developed their ovaries to continue to lay eggs in November-December (Fig. 5). On the other hand, our data on isolated animals (Fig. 2) reflect the inability of these animals to initiate egg laying in the months of November - December. To the extent that temperature may differentially affect the initiation and continuation of egg laying, this will be a confounding factor in our interpretation. In other words, we do not know at this stage whether isolated animals cannot merely begin to lay eggs in November-December or whether they cannot also continue to lay eggs in November - December in spite of having begun to lay eggs earlier. We hope to distinguish between these two possibilities in future experiments. Whatever the outcome of these expriments, an additional advantage of group life in the form of "co-operative thermoregulation" will remain in at least as far as initiation of egg laying is concerned.

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